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CAMBRIAN PETALONAMID *STROMATOVERIS* PHYLOGENETICALLY LINKS EDIACARAN BIOTA TO LATER ANIMALS

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Abstract: Macro-organisms of the Ediacaran period (635–541 Ma) were large and morphologically complex, with some living in aphotic habitats, presenting the possibility that they were early animals. However, 'bizarre' Ediacaran morphologies and mouldic preservation have frustrated comparison to later taxa. Consequently, both the positions of Ediacaran biota in the tree of life and the origins of the Metazoa have remained disputed. Here we provide phylogenetic evidence to identify Ediacaran macro-biota as animals, based on 206 new fossils of *Stromatoveris psygmoglena* from the lower Cambrian Chengjiang Lagerstätte. Exceptionally preserved soft-tissue anatomy shows that *Stromatoveris* was a soft-bodied, radially symmetric animal with multiple, sub-branched petaloids and a differentiated holdfast. Photo-referenced morphological character analysis enables phylogenetic reconstruction of a monophyletic clade designated Petalonamae, that unites *Stromatoveris* with iconic Ediacaran genera (*Rangea*, *Pteridinium*, *Ernietta*, *Swartpuntia*, *Arborea*, *Pambikalbae* and *Dickinsonia*) and is placed as sister-group to the Eumetazoa. Therefore, based on phylogenetic bracketing within the Metazoa, the Ediacaran petalonamids are established as animals. From these findings, it follows that petalonamids remained an important component of Cambrian marine ecosystems and that the metazoan radiation can be dated to a minimum age of between 558 and 571 myr.

Key words: Ediacaran, Cambrian, phylogenetics, Chengjiang, *Stromatoveris*, Petalonamae.

DESPITE considerable debate, evolutionary relationships of the Ediacaran macro-biota have remained unresolved. Suggested affinities have ranged through protozoans, algae, fungi, lichens, basal opisthokonts and stem or crown-group animals (see reviews by Antcliffe & Brasier 2007; Budd & Jensen 2017). Their monophyly has also been extensively disputed. Of the two major taxonomic hypotheses, one scatters Ediacaran taxa across extant phyla (Budd & Jensen 2017) while the other proposes a distinct clade such as phylum Petalonamae (Pflug 1972*a*) (including *Rangea*, *Arborea*, *Pteridinium* and *Ernietta*) or the 'Vendozoa' or 'Vendobionta' (Seilacher 1989) (including, amongst others, *Rangea* and other rangeomorphs (Narbonne 2004), *Pteridinium* and *Dickinsonia*). However, Ediacaran macrofossils are generally preserved as comparatively uninformative surface impressions (moulds or casts). Consequently, hypothesized animal relationships (Buss & Seilacher 1994; Jenkins & Nedin 2007; Vickers-Rich 2007; Brasier & Antcliffe 2008; Sperling & Vinther 2010; Meyer *et al.* 2014; Gold *et al.* 2015; Cavalier-Smith 2017; Hoekzema *et al.* 2017; Dufour & McIlroy 2018; Dunn *et al.* 2018; McMenamin 2018) have not previously been tested by analysis of directly preserved soft-tissue anatomy or morphological phylogeny.

The lower Cambrian (Series 2, Stage 3, 518 Ma; Yang *et al.* 2018) species *Stromatoveris psygmoglena* Shu, Conway Morris & Han *in* Shu *et al.*, 2006 was previously known from eight specimens, with noted similarities to both ctenophores and frondose Ediacaran macro-fossils. However, the presence of detailed anatomical similarities to Ediacaran taxa was subsequently questioned (Antcliffe & Brasier 2007) and *Stromatoveris* was listed as an animal of uncertain affinity in a recent review of Chengjiang fossils (Xian-Guang *et al.* 2017). *Stromatoveris* is here reinterpreted, based on 206 new fossils from the Chengjiang Konservat-Lagerstätte, Sanjiezi village, Erjie town,

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Jingning County, Kunming City, Yunnan Province, China, held in the collections of the Early-Life Institute, Northwest University, Xi'an, China. These fossils provide new insights into the comparative anatomy of *Stromatoveris*. Morphological phylogenetic analysis alongside 7 Ediacaran ingroup genera and 11, diverse outgroups then reveals that *Stromatoveris* links these members of the Ediacaran macro-biota to the animals of the Cambrian.

Institutional abbreviations. ELI, Early-Life Institute, Northwest University, Xi'an, China; NESM, National Earth Science Museum of Namibia, Windhoek, Namibia; SAM, South Australian Museum, Adelaide, Australia.

METHOD

Phylogenetic analysis

Morphological phylogenetic analysis was conducted to test the relationship of the monospecific lower Cambrian genus *Stromatoveris* to 7 hypothesized petalonamid genera from the Ediacaran period and 11 outgroups, covering protozoa, fungi, algae and animals. The Ediacaran ingroup genera were *Rangea* (the type genus for the rangeomorphs; Dececchi *et al.* 2017; Sharp *et al.* 2017), *Pteridinium*, *Ernietta*, *Swartpuntia*, *Arborea* (using the specimen classifications of the South Australian Museum which incorporate some specimens previously classified as *Charniodiscus*; Laflamme *et al.* 2018), *Pambikalbae* (originally described as a member of Petalonamae; Jenkins & Nedin 2007) and *Dickinsonia*. These genera were selected because they represent intersecting sets of taxa previously suggested to fall within a single Ediacaran clade (Pflug 1972*a*; Seilacher 1989; Jenkins & Nedin 2007; Dececchi *et al.* 2017), cover a broad range of previously suggested Ediacaran groups and recovered clades (e.g. all named clades identified in the phylogenetic analysis of Dececchi *et al.* (2017): Rangeomorpha, Arboreomorpha and Erniettomorpha) and are represented by accessioned fossil specimens with excellent preservation (including three-dimensional anatomy), facilitating morphological character analysis alongside *Stromatoveris*.

A diverse range of 11 outgroup genera were also included to test ingroup monophyly robustly (all having been previously suggested as potential relatives of ingroup taxa) and to test a wide range of potential phylogenetic placements. Outgroup genera were *Thectardis* (a proposed Ediacaran sponge; Sperling *et al.* 2011); the Cambrian sponge *Leptomitus*; the extant placozoan *Trichoplax* (Sperling & Vinther 2010); the Cambrian ctenophore (Dzik 2002; Shu *et al.* 2006; Zhang & Reitner 2006) *Galeactena*; the extant cnidarians *Pennatula* (Octocorallia, Pennatulacea) (Glaessner & Wade 1966; Antcliffe & Brasier 2007) Eocene–Recent coral *Fungia* (Valentine 1992); the extant polychaete *Spinther* (Glaessner & Wade 1966); the Cambrian chordate (Dzik 2002) *Pikaia*; the extant, terrestrial lichen *Rhizocarpon* (Retallack 2013); the Cambrian macro-alga (Ford 1958) *Bosworthia* (Wu *et al.* 2016); and the Ediacaran fossil *Palaeopascichnus*, interpreted as a giant protozoan (Seilacher *et al.* 2003; Antcliffe *et al.* 2011). For extant genera without fossil representatives, characters were coded with reference to the fossilized appearance of near relatives where possible (e.g. sea pens (Reich & Kutscher 2011), polychaetes (Conway Morris 1979)).

Morphological character analysis (the process of morphological observation and character coding for subsequent phylogenetic analysis) followed a best-practice protocol (Ramirez *et al.* 2007) including documentation of all 71 specimens on which coded morphological characters were specifically based, with a labelled photograph referenced to every character state. This yielded 42 morphological characters (40 parsimony informative) for 19 genera (8 ingroup genera; 11 outgroups). The photo-referenced morphological data matrix is available in MorphoBank (Hoyal Cuthill & Han 2018*a*) and in nexus format in Dryad (Hoyal Cuthill & Han 2018*b*). Seventy-four newly provided digital images (MorphoBank Media) are reusable under a CC BY creative commons licence. Duplicates of the project may be requested through MorphoBank for further research.

Phylogenetic character states pertinent to the hypothesis of ingroup monophyly (relative to the outgroup taxa) were coded at the level of observations on fossil morphology (for example, basal primary branch longer than apical primary branch), rather than interpretations which might follow from these observations (e.g. sub-apical primary branching during growth (Antcliffe & Brasier 2007; Hoyal Cuthill & Conway Morris 2014; Gold *et al.* 2015; Hoekzema *et al.* 2017)). Morphological characters which were quantitative in nature (e.g. width/length; Sperling *et al.* 2011) were coded based on measurements from digital photographs of documented fossil specimens (rather than qualitative assessments).

Character analysis and subsequent phylogenetic reconstruction had two primary aims. The first aim was to identify robust synapomorphies (shared derived character states) for the ingroup and the second was to establish ingroup phylogenetic positions relative to the outgroup taxa. Consequently, of the 42 total characters (Hoyal Cuthill & Han 2018*a*, *b*), 22 characters relate to the organization and structure of the petaloids and sub-branches (which make up the majority of the body in the ingroup taxa), 5 characters relate to basal attachment structures (e.g. basal stem and holdfast) and 15 characters represent fundamental morphological features (such as symmetry group and presence or absence of unit differentiation or

an internalized body cavity) that resolve the relationships of the outgroups and are comparable to the ingroup fossils (with 14 out of 15 coded as non-missing for at least one ingroup taxon). The total number of petaloids per individual was not itself included as a phylogenetic character. This is because species represented by comparatively large numbers of fossils (e.g. *Stromatoveris psygmoglena* or *Rangea schneiderhoehni*; Vickers-Rich *et al.* 2013) show that the number of visible, preserved petaloids is highly variable among specimens, making it difficult to separate potential biological variation from preservational variability.

Parsimony analysis was conducted using the program PAUP version 4b10 (Swofford 2002) with default heuristic tree search settings. Phylogenetic analyses were conducted without any ingroup/outgroup monophyly constraint. *Palaeopascichnus* was set as the outgroup for rooting the tree (alternative rooting to the alga *Bosworthia* results in no change to the recovered phylogenetic topology). Tree comparisons were conducted in PAUP using the symmetric (Robinson–Foulds) distance, which counts the number of branches that must be contracted or decontracted to convert between two trees. Clade support values were calculated using PAUP. These were the bootstrap support (fraction of character samples which support a clade, over 500 replicates, with 100 indicating the highest possible support) and the decay index (increase in tree length required before the clade is no longer supported). Shared derived character states (synapomorphies) which supported specific major clades were identified using the program SplitsTree4 (Huson & Bryant 2006).

Minimum node dates for Petalonamae and Rangeomorpha were summarized from the literature based first on only fossil taxa included in this study, and second on combined clade membership information from this phylogenetic analysis (which analyses the position of rangeomorph type genus *Rangea* (Sharp *et al.* 2017) within Petalonamae and Metazoa) and a previous, complementary phylogenetic analysis of Ediacaran species (Dececchi *et al.* 2017) (which places the oldest known rangeomorph genera *Charnia* and *Trepassia* (Narbonne & Gehling 2003) in a sub-clade, 'Rangeomorpha' with *Rangea*).

RESULTS

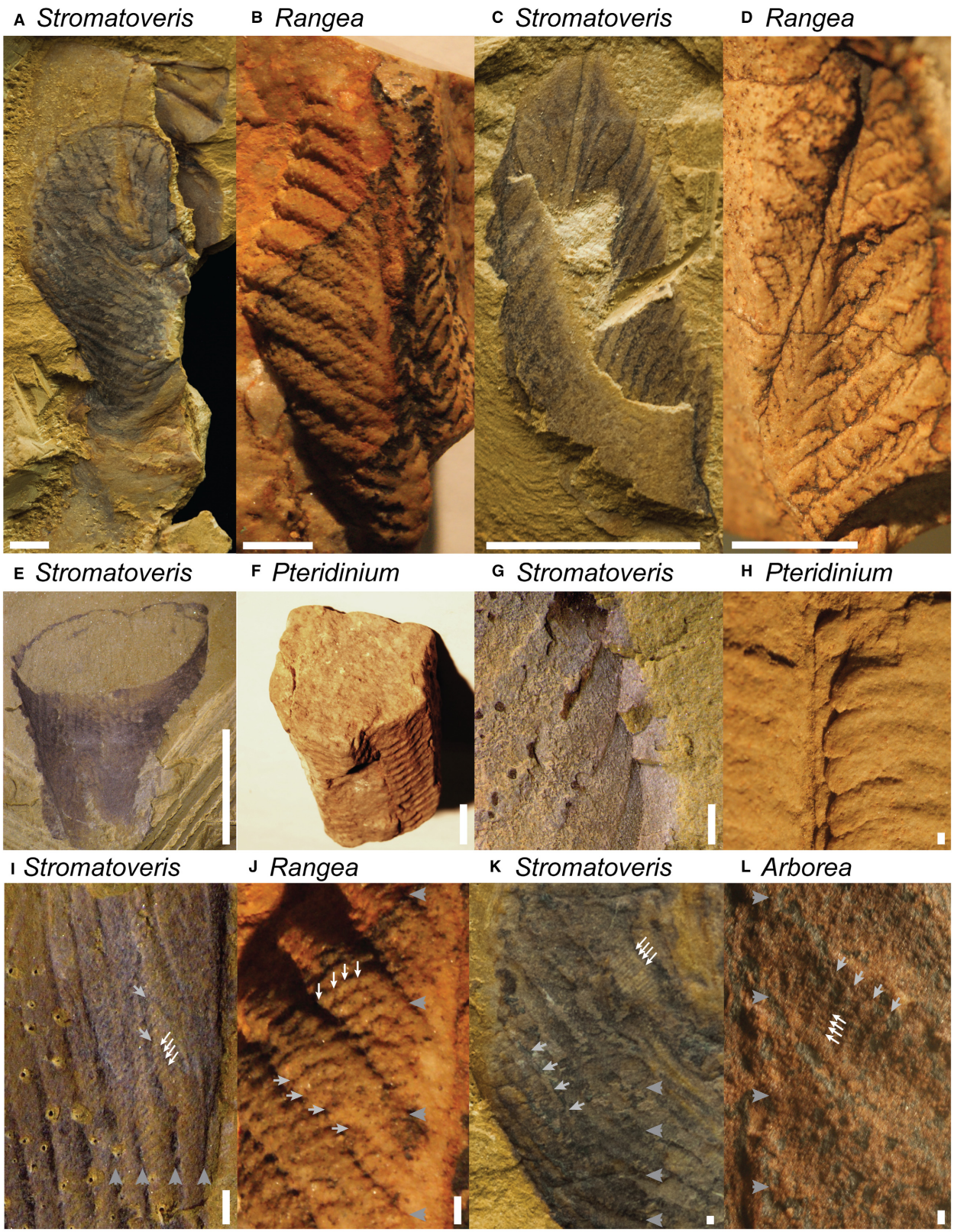
Comparative anatomy of Stromatoveris psygmoglena

Among the new specimens of *Stromatoveris*, at least two and up to four branched petaloids (or 'fronds') are visible at the fossil surface. This multi-foliate arrangement is indicated by specimens exhibiting separated or strongly delineated petaloids (Figs 1A, C; 2B, E; Hoyal Cuthill & Han 2018*b*, fig. S2), primary branching directions incompatible with a single over-folded petaloid (Figs 1C, 2E), and overprinting of different petaloids (Fig. 1C; Hoyal Cuthill & Han 2018*b*, fig. S2).

Multiple petaloids can be distinguished from subbranches (e.g. primary lateral branches within a single petaloid) because petaloids are of equal and maximal size within the organism (Fig. 2) not part of an increasing size series. Petaloids are preserved in a variety of orientations, indicating flexibility and apical and lateral freedom, and are commonly longitudinally folded and 'furled' (curved). Multiple petaloids are arranged radially, often axis-to-axis (Fig. 1A, C) suggesting that this was their life position (Fig. 2G), although positional variation (Figs 1, 2) indicates that petaloid arrangements were dynamically affected by fluid flow. These observations reveal a macroorganization shared across frondose Ediacaran biota (Figs 1, 2), for example with up to six radial, longitudinally folded petaloids identifiable in *Rangea* (four: Fig. 1D; five or six: Vickers-Rich *et al.* 2013, fig. 8).

Natural petaloid cross-sections (Fig. 1E, G) show that body tissue of *Stromatoveris* is preserved at a width of approximately 0.05–0.1 mm (after sedimentary compaction). Relatively complete specimens, reaching up to 10.5 cm in length (Fig. 1A), show a blunt basal termination where petaloids join. In some specimens, the base is buried at a lower level than the petaloid apices (e.g. Fig. 1A). This suggests *in situ* preservation with a differentiated basal region acting as a holdfast in a primarily sessile, epibenthic life habit. One specimen (Hoyal Cuthill & Han 2018*b*, fig. S1) additionally preserves a small basal expansion, highly similar in position, structure and relative dimensions to the 'axial bulb' type of holdfast observed in *Rangea* (Vickers-Rich *et al.* 2013, fig. 7), which probably aided anchorage. The great majority of the body therefore consisted of the thin, free petaloids (Fig. 1; Hoyal Cuthill & Han 2018*b*, figs S1, S2) while the small remainder was buried in sediment (Hoyal Cuthill & Han 2018*b*, fig. S1). There is, therefore, no evidence for a through-gut comparable to that of bilaterians, and little potential space for an internal digestive cavity comparable to the coelenteron of cnidarians or ctenophores (which extends through most of the body).

Stromatoveris shows striations on the petaloids, previously compared to the comb rows of ctenophores (Shu *et al.* 2006). New specimens instead show the repeatedly branched, 'feathered' organization (Fig. 1) originally proposed to characterize phylum Petalonamae (Pflug 1972*a*) and, subsequently, unranked taxon Rangeomorpha (Narbonne 2004; Dececchi *et al.* 2017) (considered here to be a sub-group of Petalonamae). The shortest primary branches are at the apex of the petaloid, consistent with sub-apical branching growth (Antcliffe & Brasier 2007; Hoyal Cuthill & Conway Morris 2014). At least three


A Stromatoveris
B Rangea
C Stromatoveris
D Rangea
E Stromatoveris
F Pteridinium
G Stromatoveris
H Pteridinium
I Stromatoveris
J Rangea
K Stromatoveris
L Arborea

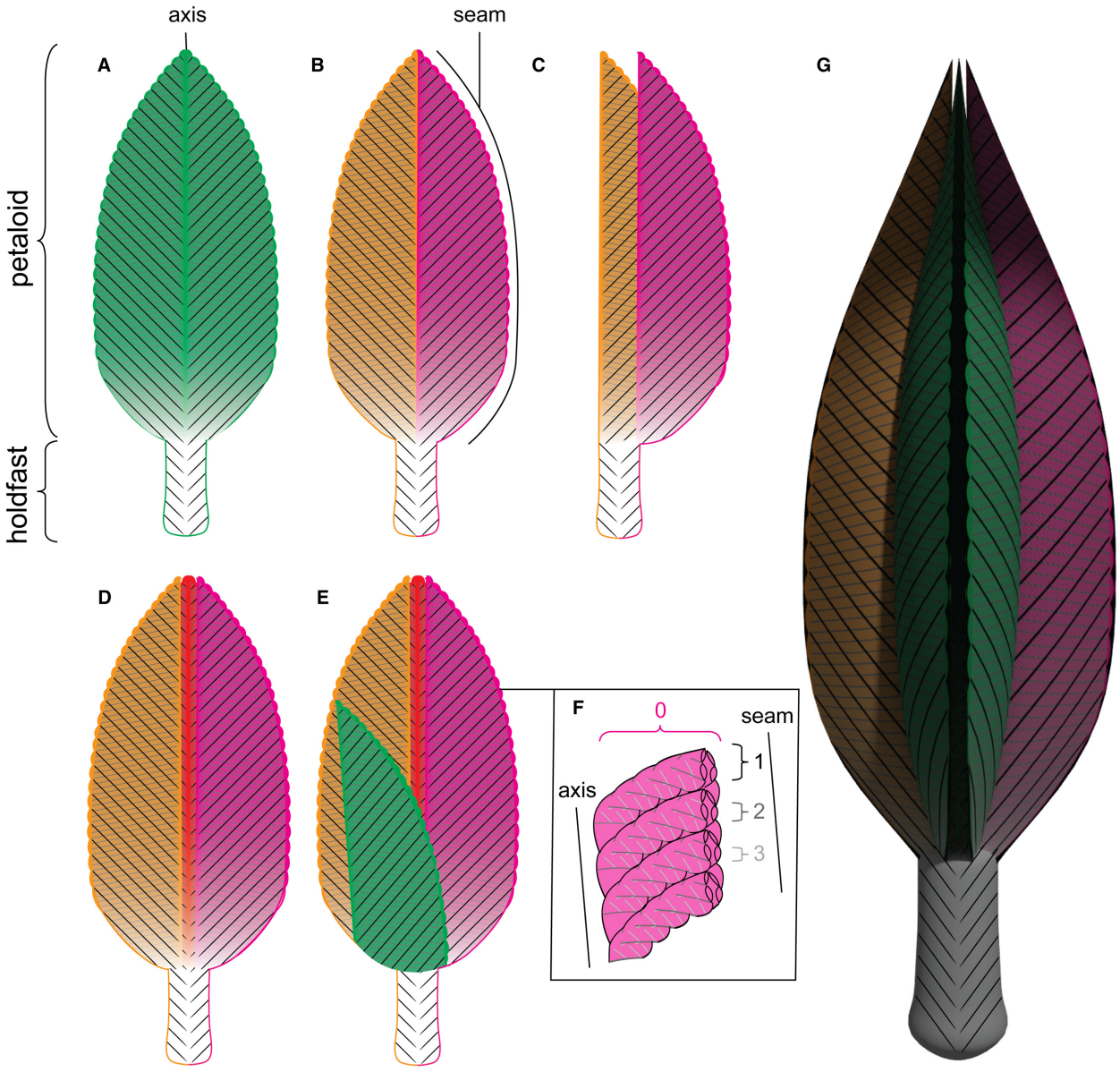


FIG. 2. Diagrams of the petalonamid body-plan exemplified by *Stromatoveris psygmoglena*. Among fossil petalonamids (Fig. 1), petaloids (indicated with distinct colours) are preserved in a variety of arrangements due to apical and lateral freedom and flexibility in life. A–E, examples of petaloid arrangements and overlay patterns inferred among fossil specimens. Number of petaloids visible in surface view: 1 (A), 2 (B–C), 3 (D), 4 (E), with one partial, displaced petaloid in green (as in specimen illustrating ch. 6 in Fig. 3). F, detail illustrating furled branches of increasing order: 0 (petaloid), 1 (primary), 2 (secondary), 3 (tertiary). G, reconstruction of *Stromatoveris* showing inferred life position of petaloids.

orders of branching are evident (primary to tertiary, Figs 1I, K, 2F). Sub-branch apices (distal to the lower order axis where branches originate) are delineated by a scalloped lateral margin on the parent branch (e.g. the petaloid at lowest, zero, order, Fig. 2F) and by surface curvature in specimens with relatively high three-

FIG. 1. Multi-foliate petalonamid taxa from the Ediacaran and Cambrian periods. Lower Cambrian *Stromatoveris psygmoglena* (new specimens): A, K, ELI:EJ-105-A; C, ELI:EJ-166-A; E, ELI:EJ-132-A; G, ELI:EJ-180-A; I, ELI:EJ-104-A (image vertically reflected for comparability). Ediacaran *Rangea* sp.: B, J, NESM:F-541; D, NESM:F-387. *Pteridinium* sp.: F, NESM:F-319; H, NESM:F349. L, *Arborea* (/*Charniodiscus*) *longus* SAM P-137 (holotype). I–L, petaloid details illustrating repeated branching. At least three orders of striation are visible (arrows). Scale bars represent: 1 cm (A–F); 1 mm (G–L).

dimensional relief (Fig. 1K). Occasionally, alternating primary branch originations are also visible (Hoyal Cuthill & Han 2018*a*, media M451664) at the petaloid axis (the 'stem', 'stalk' or zero order branch axis), although this is frequently concealed when petaloids are longitudinally folded (Fig. 1I, right). Alternate primary branching (alternating, left and right, from the central axis) is also indicated by interdigitated 'seams', where the apices of one row of primary branches are furled or folded over to meet another (Figs 1G–H, 2F). Higher order branching (secondary and above) is most often visible as a finely striated surface texture, which marks the longitudinal boundaries between sub-branches (e.g. Fig. 1K upper region). Exceptional *Stromatoveris* specimens retain areas of three-dimensional branching detail to at least tertiary level (Fig. 1I, K). However, some *Stromatoveris* specimens, or parts of specimens (e.g. Fig. 1A, upper region), are smooth (with entirely effaced surface texture) indicating that observed subdivision can be preservationally limited, as in Ediacaran taxa such as *Rangea* (Hoyal Cuthill & Han 2018*a*, media M451601). Sediment often infills furled petaloids and the spaces between them (Fig. 1E). These spaces vary in size and shape, indicating considerable petaloid flexibility (Figs 1, 2). Furled primary branches can also enfold a sediment filled, longitudinal space (approximately self-similar to that of the whole petaloid) for example, with roughly oval to tear-shaped cross-section (Fig. 1G).

These observations indicate that the branches of a given order (e.g. primary) met at their lateral margins to form a sheet-like structure (e.g. the petaloid at the lowest branching order). Frequently, this was then longitudinally folded at the central axis and furled so that the exterior lateral margins met at an interdigitating branch seam. Repetition at higher branch orders created a self-similar system of tube-like furled sheets, somewhat comparable to the 'quilted pneu' structure proposed by (Seilacher 1989). However, unlike closed tubes, branch seams were open to the external seawater at multiple locations and size scales, permitting through-flow of nutrient carrying fluid. Evidently, during burial, sediment could also enter through the open seams (Fig. 1E, G).

Stromatoveris specimens were occasionally found in close association with algae (*Sinocylindra yunnanensis*) and brachiopods (*Lingulella chengjiangensis*). In one case, the pedicle of a brachiopod contacts the margin of a *Stromatoveris* specimen, compatible with attachment as an epibiont (Hoyal Cuthill & Han 2018*b*, fig. S3).

EDX spectroscopy of three *Stromatoveris* specimens (ELI:180-A, ELI:287-B, ELI:JS-298-A) measured carbon (at 11–14%), as well as oxygen (64%), silica (12–14%) and aluminium (6–7%), consistent with the presence of clay minerals, potassium (2%), iron (<2%) and very low levels of calcium (<0.1%).

Phylogenetic relationships of Stromatoveris *and Ediacaran biota*

Photo-referenced character analysis (Ramirez *et al.* 2007), with character coding based on 71 documented specimens and 102 digital media, produced a character–taxon matrix of 42 morphological characters (40 parsimony informative) for 19 genera. Twenty-seven characters describing details of petalonamid morphology are illustrated by photo-referenced examples in the main manuscript (Fig. 3). All character–taxon data and associated media are provided in Hoyal Cuthill & Han (2018*a*), where the photo-referenced character matrix, associated labels, specimen media, documentation and museum classifications can be viewed and downloaded. The character–taxon matrix is also provided in nexus format in Hoyal Cuthill & Han (2018*b*).

Morphological phylogenetic analysis using parsimony recovered a monophyletic clade, which we designate Petalonamae (following Pflug (1970*a*, *b*, 1972*a*, *b*), including both Cambrian *Stromatoveris* and seven iconic members of the Ediacaran biota (Fig. 4). Analysed alongside a wide range of outgroup taxa, the petalonamids were found to be monophyletic in both recovered trees (which show identical ingroup topologies; Hoyal Cuthill & Han 2018*b*, appendix S2), with Petalonamae placed as the sister-taxon to the Eumetazoa. Phylogenetic analysis of the petalonamids alone recovers the same ingroup topology. Recovered ingroup clades reflect several noted similarities between Ediacaran petalonamids (Jenkins & Nedin 2007; Brasier & Antcliffe 2008; Dececchi *et al.* 2017) while additionally incorporating *Stromatoveris*. For the five genera that overlap with a recent phylogenetic analysis of Ediacaran species (Dececchi *et al.* 2017, fig. 1) our analysis, based on independently coded characters and a different set of ingroup and outgroup taxa, recovers a very similar phylogenetic topology. Phylogenetic topologies for these five overlapping taxa differ in the placement of only one taxon (symmetric distance = 4), with our analysis placing *Swartpuntia* outside a clade including *Rangea*, *Pteridinium*, *Ernietta* and *Arborea* (rather than outside a clade of *Ernietta* and *Pteridinium*; Dececchi *et al.* 2017, fig. 1). Phylogenetic monophyly, placement, age, and lack of demonstrated descendants (though see discussion in Budd & Jensen 2017) support taxonomic ranking of Petalonamae as a distinct animal phylum (Pflug 1972*a*).

DISCUSSION

The relatively complex body plan of the Petalonamae combined basal/apical differentiation, radial petaloid symmetry typical of basal metazoans of grade 'Radiata'

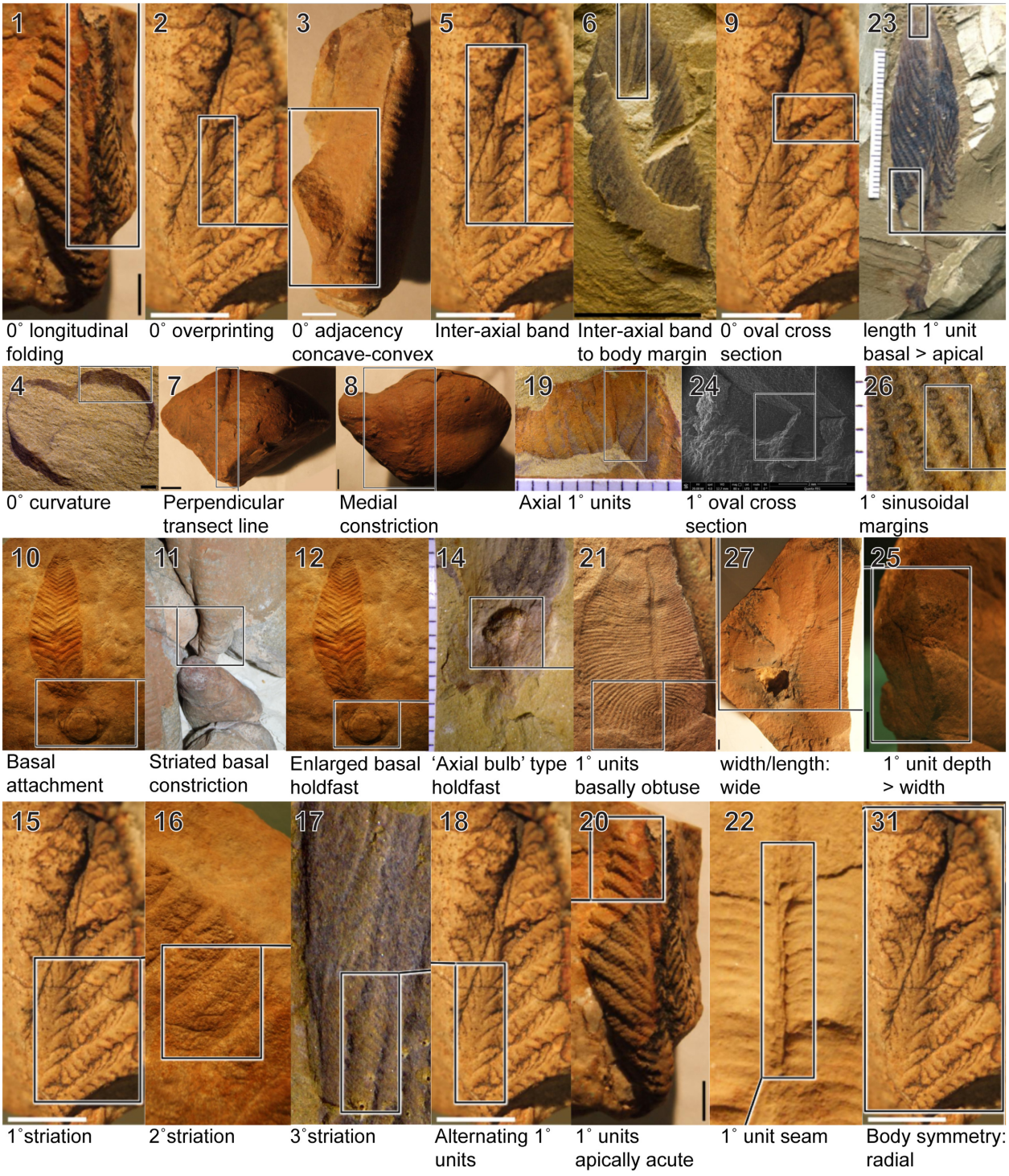


FIG. 3. Photo-referenced examples for 27 morphological characters of the Petalonamae. Labelled images for all 42 morphological characters across all 19 taxa are available in Hoyal Cuthill & Han (2018*a*). Character numbers correspond to those of the character–taxon matrix (Hoyal Cuthill & Han 2018*a*, *b*). Character names abbreviated; labels 0°, 1°, and 2° indicate, respectively, structural units of zero (petaloid), primary and secondary order. All character states illustrated are present unless otherwise indicated. Images show fossil specimens of *Stromatoveris* (characters 6, 23, 4, 19, 24, 26, 14, 17) *Rangea* (1, 2, 5, 9, 15, 18, 20, 31), *Pteridinium* (3, 11, 22), *Ernietta* (7, 8), *Arborea* (10, 12, 25, 16), *Dickinsonia* (21) and *Swartpuntia* (27). Scale bars represent 1 cm, except for characters: 4 (1 mm); 19, 26, 14, 23 (mm scale); 24 (2 mm); 10, 12 (specimen length 40 cm); 11 (display specimen, not measurable).

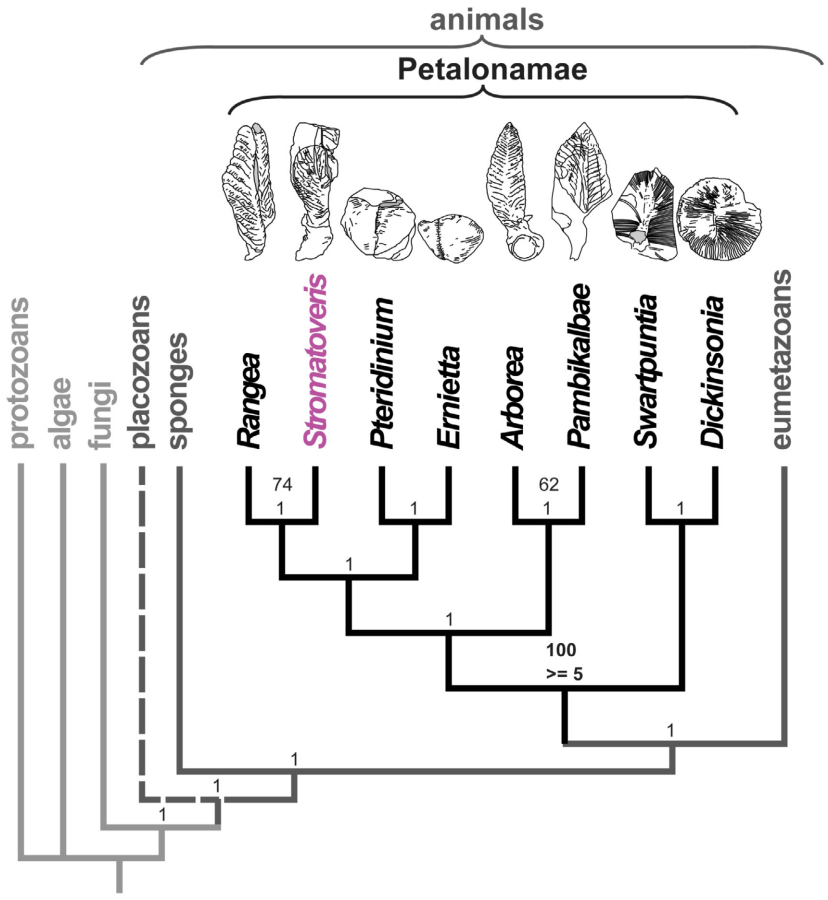


FIG. 4. Phylogeny of the Petalonamae. Phylogeny reconstructed using parsimony analysis of 42 photo-referenced morphological characters (Hoyal Cuthill & Han 2018*a*, *b*). Strict consensus topology shown for two most parsimonious trees (outgroup clades condensed, full outgroup topologies in Hoyal Cuthill & Han 2018*b*, appendix S2). Tree length = 66, consistency index CI = 0.65 and retention index RI = 0.85. Upper numbers show bootstrap support values (>50); lower, decay index. Support values for clade Petalonamae are shown in **bold**. Outgroups shown in grey. Outgroup placozoan *Trichoplax* was recovered as a basal animal (dashed line) although eumetazoan placement (indicating morphological reduction) is supported by genomic data (Pisani *et al.* 2015).

(Vickers-Rich 2007), alternate sub-branching within each petaloid (Antcliffe & Brasier 2007; Brasier & Antcliffe 2008; Hoyal Cuthill & Conway Morris 2014) and inferred sub-apical branch origination (Hoyal Cuthill & Conway Morris 2014; Gold *et al.* 2015; Hoekzema *et al.* 2017). This organization, as well as evidence in *Dickinsonia* (Ivantsov & Malakhovskaya 2002; Gehling *et al.* 2005; Sperling & Vinther 2010; Gold *et al.* 2015) for active body

TABLE 1. Morphological characters supporting major clades identified in this study.

Clade	Supporting character	Character number
Petalonamae (inclusive of *Stromatoveris*)	**Zero order unit longitudinal folding**	1
	Zero order unit concave-convex adjacency	3
	Zero order unit curvature (furling)	4
	Inter-axial band	5
	Inter-axial band reaching body margin	6
	Zero order unit approximately tear-shaped cross section	9
	Tertiary striation of secondary units	17
	Alternating primary units (at axis)	18
	Primary units interdigitated at seam	22
	Primary unit approximately tear-shaped cross-section	24
Petalonamae + Eumetazoa (Cnidaria, Ctenophora, Bilateria, Placozoa)	Active movement	41
	Locomotion	42
Metazoa (inclusive of Petalonamae)	Active movement	41

Shared derived characters (synapomorphies) supporting listed clades identified using the program SplitsTree4. Diagnostic characters of Phylum Petalonamae shown in **bold**.

TABLE 2. Summary of published geochronological age data for petalonamid fossils and their higher taxa.

Taxon	Taxonomic rank	Dated fossil occurrence range (Ma)	Datum type
Stromatoveris psygmoglena	Species	518.03 ± 0.71 (Yang *et al.* 2018)	Species occurrence
Rangea	Genus	552.85 ± 0.77 (Boag *et al.* 2016)	Genus occurrence
Dickinsonia	Genus	558 ± 1 – 551 ± 4 (Boag *et al.* 2016)	Genus range
Rangeomorpha	Unranked clade (Dececchi *et al.* 2017)	552.85 ± 0.77 (Boag *et al.* 2016)	Occurrence of phylogenetic clade member
Rangeomorpha	Unranked clade (Dececchi *et al.* 2017)	570.94 ± 0.38 (Pu *et al.* 2016) – 552.85 ± 0.77 (Boag *et al.* 2016)	Range of clade members, using combined phylogenetic information
Petalonamae	Phylum	558 ± 1 – 518.03 ± 0.71 (Yang *et al.* 2018)	Range of phylogenetic clade members
Petalonamae	Phylum	**570.94 ± 0.38** (Pu *et al.* 2016) – **518.03 ± 0.71** (Yang *et al.* 2018)	Range of clade members, using combined phylogenetic information

Incorporation of Petalonamae provides minimum age data for the Metazoa based on geochronological radiometric dates for fossil occurrences. Age ranges for clades based, first, on only fossil genera included in this phylogenetic study and, additionally, on incorporated clade membership information from a previous phylogenetic analysis of Ediacaran species (Dececchi *et al.* 2017). The maximum range estimate, based on published radiometric dates and all available phylogenetic information, is shown in **bold**.

locomotion, supports phylogenetic placement as a monophyletic clade of crown-group animals (Fig. 4; diagnostic synapomorphies Table 1) located above sponges, as the sister-group to the Eumetazoa (as represented here by Bilateria, Cnidaria and Ctenophora; e.g. Pisani *et al.* 2015) (Buss & Seilacher 1994; Jenkins & Nedin 2007; Vickers-Rich 2007; Brasier & Antcliffe 2008; Sperling & Vinther 2010; Dufour & McIlroy 2018). Within this cladistic framework (Fig. 4; Table 1), active, supracellular (Bond & Harris 1988), body locomotion can be seen to represent a key case of a eumetazoan synapomorphy (associated with numerous physiological and microstructural innovations; Nickel 2010) which can be inferred from macro-scale Ediacaran fossils (Ivantsov & Malakhovskaya 2002; Gehling *et al.* 2005).

Petalonamids show similarities to numerous other extinct and extant taxa with which they have been previously compared. However, they show far more similarities to each other (Pflug 1972*a*; Seilacher 1989) than to any external clade, indicating that several wider similarities are convergent (Brasier & Antcliffe 2008). A relatively small number of fundamental morphological characters (and associated behaviours) are necessarily crucial to determining the relationships between the disparate animal phyla. Consequently, every available character is of evidential importance for the phylogenetic position of the Petalonamae within the animals. Given the strong morphological character support for their monophyly, however, the characteristics of individual petalonamid species and specimens should, in future, be evaluated within this wider comparative context (Fig. 4; Table 1).

In conclusion, we identify previously enigmatic members of the Ediacaran biota as animals (*Rangea*, *Pteridinium*, *Ernietta*, *Swartpuntia*, *Arborea*, *Pambikalbae* and *Dickinsonia*) based on phylogenetic bracketing of the petalonamids within the Metazoa (Fig. 4) as well as the undisputed animal status of *Stromatoveris* (Shu *et al.* 2006; Xian-Guang *et al.* 2017). Incorporation of phylum Petalonamae provides minimum age constraint data for the Metazoa at the first appearances of petalonamid fossils (Table 2), the oldest of which are the rangeomorphs (Narbonne 2004; Dececchi *et al.* 2017) with the first known species appearing at approximately 571 Ma (Narbonne & Gehling 2003; Pu *et al.* 2016).

Observed co-occurrences with algae and brachiopods (Hoyal Cuthill & Han 2018*b*, fig. S3) unambiguously indicate an aquatic, and probably shallow marine (Xian-Guang *et al.* 2017), habitat for *Stromatoveris*. Associated brachiopods, as well as an abundance of sponges in the wider Chengjiang community (Xian-Guang *et al.* 2017) indicate relatively high levels of organic material compatible with heterotrophic feeding in *Stromatoveris*, also suggested for Ediacaran petalonamids for example via osmotrophy of dissolved organic carbon (Laflamme *et al.* 2009).

With 214 known specimens representing 1% of the locality total, *Stromatoveris psygmoglena* demonstrates that at ~518 Ma petalonamids were neither extinct (Seilacher 1989; Laflamme *et al.* 2013) nor comparatively rare (e.g. abundance <0.5%; Caron & Jackson 2006; Xian-Guang *et al.* 2017) and therefore remained an important component of lower Cambrian marine ecosystems.

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DATA ARCHIVING STATEMENT

Data and supplementary information (including character–taxon matrix and reconstructed phylogenetic trees) for this study are available in MorphoBank: http://morphobank.org/permalink/?P2695 and the Dryad Digital Repository: https://doi.org/10.5061/dryad.5pv4qm3.

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